Functional Group Responses to Reciprocal Plant Litter Exchanges between Native and Invasive Plant Dominated Grasslands

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Manipulating plant litter to direct successional trajectories is rarely considered as a management strategy. Our objective was to determine the influence of litter from an intact native plant community on a community dominated by an invasive species within the same habitat type as well as the influence of litter from a community dominated by an invasive species on an intact native plant community. We hypothesized that litter amount, type (source), and fragment size would influence various functional groups within a native plant community differently than within a weed-dominated plant community. We used reciprocal plant litter exchanges between native and invasive plant–dominated grasslands to gain an initial understanding of litter's influence on the density and biomass of native grasses, native forbs, common St. Johnswort, and downy brome. Common St. Johnswort was not influenced by any treatment. Native grass density increased with application of low (454 g/m²) amounts of litter where the grasses were subordinate to common St. Johnswort, and adding native plant litter to the weedy site nearly doubled native grass biomass. Low amounts of finely fragmented litter and high amounts of coarse litter induced native forbs to produce about twice the biomass as found in the non–litter-amended controls. Our study suggests that plant litter may be a component of vegetation that can be managed to shift the plant community toward those plants that are desired.

Nomenclature: Downy brome, *Bromus tectorum* L., common St. Johnswort, *Hypericum perforatum* L. **Key words:** Native plant–dominated grasslands, invasive plant–dominated grasslands, ecological processes, litter management.

Plant litter can play a subtle to strong role in successional dynamics because it influences many abiotic and biotic properties of the ecosystem and those ecological processes related to them (Bobbink et al. 1988; Heil and Bruggink 1987; Xiong and Nilsson 1999). Litter can affect shading, soil evaporation, temperature, decomposition rates, microbial activity, nutrient cycling, germination, and seedling establishment (Vasquez et al. 2008). The ability to influence these key processes is central to restoration and invasive plant management (Krueger-Mangold et al. 2006). However, predicting the influence of litter on plant community dynamics has been difficult because litter influences so many processes, directly and indirectly, and

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vegetation responses are a summation of a series of complex, multi-directional processes and interactions.

Some generalities about the effects of litter on vegetation have been reported (Xiong and Nilsson 1999), but they depend on the amount of litter, type of litter, and the size of litter fragments. Unfortunately, these generalities are not well tested and deviations from them are frequent. For example, a modest number of studies suggest that the negative effects of plant litter on the growth of vegetation generally outweigh the positive ones, and that vegetation growth can be reduced as a result of higher litter quantities (Violle et al. 2006; Xiong and Nilsson 1999). Conversely, some studies show that litter favors plant production by such mechanisms as conserving water during dry conditions or adding nutrients, particularly in grassland systems (Facelli and Pickett 1991a; Fowler 1986; Schlatterer and Tisdale 1969).

Difference in litter type can create differences in light, temperature, and moisture conditions of soil and lower portions of plant canopies (Facelli and Pickett 1991a). Along with litter C: N ratio, the type, or source, of litter can also alter nutrient availability and release of allelopathic

Interpretive Summary

Enduring invasive plant management will require that managers modify the ecological processes that direct successional dynamics and invasion. Plant litter affects many of those processes and managing litter could provide many practical ways of directing plant communities toward those that are desired. To the limits of our knowledge, litter amount, the type of litter, and the size of the litter fragments and their associated processes can be modified to achieve land use objectives. This investigation was aimed at determining if there was enough positive response to warrant further investigations of the ecological relationships between litter and vegetation responses. In this study, we found that low amounts of native plant litter doubled native grass biomass in areas where common St. Johnswort dominated. Native forbs were also favored with specific levels of litter. In the future, it may be possible to use management tools, such as fire, grazing, and mowing to alter litter amount, type, and size of fragments to facilitate plant community dynamics away from invasive species and toward native plant communities. We believe that future studies intended to elucidate the actual mechanisms and the role litter quality and other interactive variables (i.e., nutrient cycling, litter decomposition, C: N ratios) play in directing vegetation response are warranted.

chemicals into the soil that vary depending on decomposition rates (Ahlgren and Ahlgren 1981). Because decomposition rates vary, in part, with the amount of surface area of the litter, fine fragments may decompose faster than coarsely fragmented litter thereby influencing the rate of chemical release (Ellsworth et al. 2004).

Nonindigenous plants alter the ecological processes that direct successional dynamics and ecosystem function (Belnap et al. 2005; Cox 1999; Sheley et al. 1996; Wardle et al. 1997). Invasive plants have altered nutrient cycles (Huenneke et al. 1990; Mack and D'Antonio 2003; Stubbs and Pyke 2005), hydrologic cycles (Lacey et al. 1989), and energy flow through the system (Randall 1996). Invasive species can develop a feedback mechanism that favors their own populations by altering ecological processes (Evans et al. 2001; Klironomos 2002; Rimer and Evans 2006). For example, downy brome (Bromus tectorum L.) generates a positive feedback loop by acquiring and assimilating subsurface nitrate and depositing it at the surface as litter, where decomposition and leaching return that nitrogen to subsurface layers where it is again available for uptake by downy brome (Sperry et al. 2006). In one form or another, litter is related to most of the ecological processes associated with invasion in many ecosystems (Krueger-Mangold et al. 2006; McLendon and Redente 1991).

Influences of plant litter on community dynamics have rarely been studied in rangeland environments, and most litter studies have examined one species of litter influencing germination, seedling growth, or biomass of another species (Bosy and Reader 1995; Olson and Wallander 2002). In those studies, no unified theories about litter

have emerged and mainly negative responses, with some positive responses, are documented. For example, in a greenhouse, Bosy and Reader (1995) studied the effects of 715 g/m² of Kentucky bluegrass (*Poa pratensis* L.) shoot litter on four forbs, including common St. Johnswort (Hypericum perforatum L.). They found germination of all species except common mullein (Verbascum thapsus L.) was reduced by 26 to 41% compared to a no-litter control. Olson and Wallander (2002) found that spotted knapweed (Centaurea maculosa auct. non Lam.; = C. stoebe L. ssp. micranthos (Gugler) Hayek) litter did not affect seed germination, seedling growth, or seedling survival of bluebunch wheatgrass [Pseudoroegneria spicata (Pursh) A. Löve]. However, seedling height was tallest with spotted knapweed litter and shortest without it, which may be a beneficial response of wheatgrass to knapweed litter that did not occur with leafy spurge litter (Olson and Wallander 2002).

Plant litter amount, type, and fragment size can influence processes across temporal, spatial, and organismal scales that influence various species based on their particular traits (Harper 1977; Xiong and Nilsson 1999). Consequently, manipulating the type, amount, and texture of litter in an attempt to direct successional trajectories is rarely considered as a management strategy. However, to be a useful tool for management, advances in our understanding of plant community responses to litter are required. For example, in this study we assess the effects of litter from plant assemblages, including nonnative invasive plants, on plant community dynamics. Our objective was to determine the influence of litter collected from an intact native plant community on a community dominated by an invasive species within the same habitat type as well as the influence of litter collected from a community dominated by an invasive species on an intact native plant community. We used reciprocal plant litter exchanges between nativeand invasive plant-dominated grasslands to gain an initial understanding of litter's influence on the density and biomass of native grasses, native forbs, common St. Johnswort, and downy brome. We do not attempt to discern the mechanism (or mechanisms) driving plant response because the paucity of existing data on functional groups' responses to litter from entire plant communities make developing a rational mechanistic hypothesis nearly impossible. In this study, we hypothesized that litter amount, type, and fragment size would influence various functional groups (C3 grass, C4 grass, forb, legume, woody species) within a native plant community differently than within a weed-dominated plant community.

Materials and Methods

Study Site. This study was conducted on the National Bison Range refuge located approximately 64 km north of

Missoula, MT (47°21′N, 114°11′W; T 18 N, R 20 W, sec 6). The area has been continuously grazed by bison since 1908. The bison herd ranges from 350 to 450 animals over the 18,500-acre refuge. The elevation is 960 m and the area receives an average annual precipitation of between 380 and 480 mm, with peaks in the winter and spring. Soils are a Niarada gravelly loam, which is a mixture of Niarada (Loamy-skeletal, mixed, superactive, fridid Calcic Haploxerolls and Jocko (Sandy-skeletal, mixed, frigid Calcic Haploxerolls) soils.

In this reciprocal plant litter exchange study, two adjacent sites were selected within the refuge: one outside and one inside an area excluded from bison grazing for over 40 yr. Both sites lay in a rough fescue (Festuca scabrella Torr. ex Hook.)-bluebunch wheatgrass [Agropyron spicatum (Pseudoroegneria)] plant association, which is widespread throughout the northwestern United States (Mueggler and Stewart 1980). However, the plant community outside the exclosure (where grazing occurred) was in a native late-seral stage, dominated by rough fescue (Festuca hallii (Vasey) Piper; = F. scabrella Torr. ex Hook.) and bluebunch wheatgrass (Pseudoroegneria spicata) with a subordinate group of graminoids including Sandberg's bluegrass (Poa secunda J. Presl; = P. sandbergii Vasey.), black grama (Bouteloua eriopoda (Torr.) Torr.), and 14 other native species. Native forbs included Pennsylvania cinquefoil (Potentilla pensylvanica L.), western yarrow (Achillea millefolium L.), hoary balsamroot (Balsamorhiza incana Nutt.), tapertip hawksbeard (Crepis acuminata Nutt.), and 24 other species commonly found on this habitat type. In contrast, inside the exclosure, the plant community was dominated by common St. Johnswort (> 100% cover) with representative native species from within the habitat type at low densities. Downy brome was scattered in small patches throughout the entire landscape.

Treatments and Experimental Design. Treatments were two litter types (native, weedy), two litter amounts (454 and 908 g/m²), and two sizes of litter fragments (fine, coarse). Litter addition treatments were structured factorially and applied to both sites. A no-litter treatment was included as a control. Treatments were replicated four times and placed in a randomized-complete-block design at each site. Thus, there were 2 (litter type) \times 2 (litter amount) \times 2 (litter size) \times 4 (replication) plus 4 controls for a total of 36 experimental plots at each site. The size of each experimental plot was 1 m². The plots outside the exclosure were fenced off to prevent grazing during the study.

Procedures. In October 1999 and July 2000, we collected litter from areas adjacent to each set of plots. Thus, plant litter was applied to the same plots for two years prior to sampling the third year. Litter was taken from the same area as the plots and therefore, the species composition of

the litter was proportional to the entire area. Aboveground plant material was collected to about 2.5 cm (1 in) above the soil surface. "Native" litter was that collected from outside the exclosure, whereas "weedy" litter was that collected from inside the exclosure. Because litter was collected in July 2000, there were few viable seeds in the litter for that year. "Fine" litter (< 7.6 cm long) was collected using a mulching mower with a collection bag. "Coarse" litter (> 7.6 cm long) was collected by physically hand-clipping plant material. A litter type of each size was then weighed in the field to either 454 or 908 g (1 or 2 lbs) fresh weight, which is typical of the spectrum of annual net primary productivity found in this system. Each factorial combination of litter type, size, and weight was applied to 1-m² plots at each site by broadcasting immediately after collection and weighing.

Sampling. In July 2001, density of each species within each plot was counted in three randomly located 20 × 50 cm subplots. Aboveground biomass was clipped to 2.5 cm in the entire plot, dried in a drying oven at 60 C (140 F) for 48 h, and weighed. Temperature and illuminance were measured each year for each experimental unit on the date litter was applied. Both temperature and illuminance data were collected block by block to account for variation throughout the sampling period and were accounted for in the blocking error term during analysis. Soil temperature was measured 40 mm into the soil, and the surface temperature was measured just beneath the litter layer. Illuminance was measured with a lux meter just below the litter layer about 10 mm above the soil surface.

Analysis. All data were analyzed with least square means ANOVA. For temperature and illuminance, ANOVA was conducted as a split-split plot in time using Proc Mixed.² Because the sites were not replicated, sites are not considered as fixed factors in this study. Therefore, inferences relative to sites are restricted specifically to the two sites used in this investigation. However, the other fixed effects are compared over those two sites. Rep (site) was used as the error term for site. Litter type X litter amount × litter size × rep (site) was used as the error term for litter type, litter amount, litter size within site. Year by rep (site) was used as the error term for testing year and year by site. The residual error was used for other interactions with year. Prior to analysis, data were tested for normality and equality of variances. Based on diagnostic plots, the only data that did not meet the assumption of normality and homogeneity of variance were downy brome in the control plots and nonnative forbs, which had too many zeros to be normally distributed, and these data were not analyzed. Standard errors (SE) of the means are presented along with values from F tests, means, and standard errors. Mean separations were achieved using

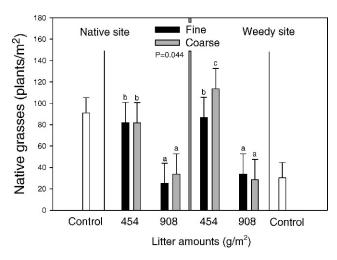


Figure 1. Interaction of litter amount, litter fragment size, and site on native grass density. Means followed by the same letter are not significantly different. Error bars equal the SEM (n = 4).

honestly significant differences ($\alpha=0.05$) procedures and means followed by the same letter are not significantly different. Because the study included three factors and two levels of each factor, the control was excluded from the factorial ANOVA. This minimized the variation in the data allowing for interaction comparisons between litter type, amount, and fragment size. However, the control means are presented with SEs for comparison. Data presented are averaged over factors that were not significant or did not interact.

Results

Native Grasses. Native grass density depended upon the interaction of site, litter amount, and litter size ($F_{1,42}$ =

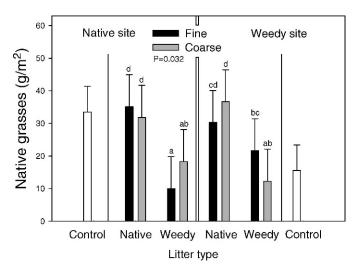


Figure 2. Interaction of litter type, litter fragment size, and site on native grass biomass. Means followed by the same letter are not significantly different. Error bars equal the SEM (n = 4).

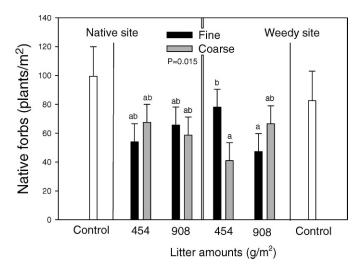


Figure 3. Interaction of litter amount, litter fragment size, and site on native forb density. Means followed by the same letter are not significantly different. Error bars equal the SEM (n = 4).

4.312, P = 0.044; Figure 1). On the native site, the control had 90 grass tillers/m². Plots receiving low amounts (454 g/m²) of litter produced 80 grass tillers/m², but adding high amounts (908 g/m²) of either litter type or size reduced native grass density by 70%. On the weedy site, the control had about 28 grass tillers/m². Plots receiving high amounts of litter produced from 22 to 30 grass tillers/m². Adding low amounts of fine litter increased native grass density to 80 grass tillers/m², whereas adding low amounts of coarse litter increased native grass density to 107 grass tillers/m² on the weedy site.

Native grass biomass was influenced by the interaction among site, litter type, and the size of the litter fragments ($F_{1,42}=4.921$, P = 0.032; Figure 2). On the site dominated by native species, the non–litter-amended control had 33 g/m². Plots receiving litter collected from the native sites produced between 30 and 34 g/m², regardless of litter size. Any amount of fine or coarse litter from the weed-dominated site decreased grass biomass by 50% of that grown with native litter on the native-dominated site. On the weed-dominated site, native grass biomass was 15 g/m² in the control, and between 12 and 20 g/m² where weedy litter was added. Adding native plant litter on the weed-dominated site increased native grass biomass to 30 g/m² compared to the control plots.

Native Forbs. The effects of litter on native forb density depended upon the site, the amount of litter, and the size of litter fragments ($F_{1,42} = 6.434$, P = 0.015; Figure 3). On the site dominated by native species, the non-amended control had just under 100 native forb plants/m². Plots receiving any amount or size combination of litter produced less than 65 native forb plants/m² and there were no differences among those means. There were about

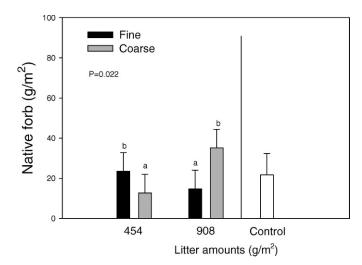


Figure 4. Interaction of litter amount and litter fragment size on native forb biomass. Means followed by the same letter are not significantly different. Error bars equal the SEM (n = 4).

80 native forb plants/m² in the control plots on the weedy site. On that site, plots with low amounts of fine litter and high amounts of coarse litter produced 78 and 67 forb plants/m², respectively.

Native forb biomass was affected by the amount and size of litter ($F_{1,42} = 5.658$, P = 0.022; Fig. 4). The control plots produced 22 g/m² of native forb biomass. Plots that received low amounts of finely fragmented litter and high amounts of coarse litter produced about 20 and 30 g/m² of native forb biomass, respectively. Plots receiving low amounts of coarse litter and high amounts of fine litter produced 10 and 11 g/m² of native forb biomass, respectively.

Common St. Johnswort. The density of common St. Johnswort depended upon the main effect of site. On the weedy site common St. Johnswort produced 33 plants/m² (SE = 7.8), but produced only 2.4 plants/m² (SE = 7.8; P = 0.031) on the native site. The biomass of common St. Johnswort was not affected by site or any litter treatment. The overall biomass was 20 g/m^2 (SE = 1.6) (data not shown).

Downy brome. Although downy brome biomass was not affected by litter treatments, downy brome density was influenced by the interaction of litter type and fragment size ($F_{1,42} = 4.446$, P = 0.041) (data not shown). The patchy distribution of downy brome made assessing the data from control plots nearly impossible because only one plot on each site had downy brome. On the native plant-dominated site, one of the four control plots had 36 downy brome plants/m²; there were 7 plants/m² on the weedy site. However, data from litter-treated plots had a normal distribution. Plots receiving finely fragmented litter produced about 4.5 (SE = 0.97) downy brome plants/

 m^2 , regardless of whether it was native or weedy litter. Weedy coarse litter increased downy brome density to 5.5 (SE = 0.97) plants/ m^2 , whereas native coarse litter decreased downy brome to 3.8 (SE = 0.97) plants/ m^2 .

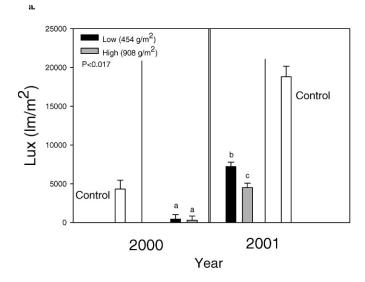
Luminance Beneath the Litter Laver. The amount of illumination measured beneath the litter (soil surface) was influenced by the interaction of year and the type of litter applied ($F_{1,42} > 12.516$, P < 0.001) as well the interaction of year and amount of litter ($F_{1,42} = 6.178$, P = 0.017). Control plots received 4,295 (SE = 1,173) lux in 2000 and 18,804 (SE = 1,367) lux in 2001 at the soil surface(Figure 5a). In 2000, any amount of litter added to plots reduced illuminance to below 500 lux. However in 2001, the high amount of litter received about 35% less light than the low litter application. Across litter amount and fragment size, litter collected from the native plant litter site and the weedy plant litter dominated site received about 100 and 600 lux, respectively, below the litter layer in 2000 (Figure 5b). In 2001, plots that had been amended with native plant litter were receiving about 2,000 lux, whereas those amended with weedy plant litter were receiving 9,600 lux. In 2000, the amount of light reaching the plant layer was below 650 lux regardless of litter amount.

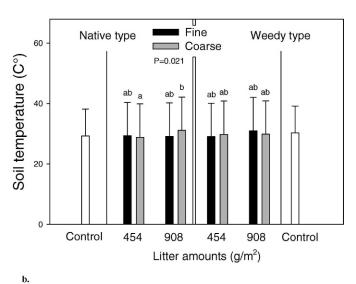
Soil and Surface Temperature. Soil temperature was influenced by an interaction among litter type, amount, and fragment size ($F_{1,42} = 5.751$, P = 0.021; Figure 6a). The only factor that accounted for the three-way interaction was on the native site where low amounts of added coarse litter had a lower soil temperature than high amounts of coarse litter. Temperature just beneath the litter layer depended upon the amount and size of the litter fragments ($F_{1,42} = 6.434$, P = 0.015; Figure 6b). Low amounts of fine litter produced the coolest environment beneath the litter layer, whereas high amounts of fine litter produced the warmest environment.

Discussion

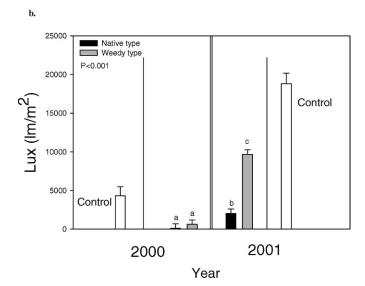
Litter plays a critical role in nutrient cycling (Nilsson et al. 1999). Land and resource managers have recognized the need to maintain enough litter to promote a sustainable nutrient status in the system (Marschner and Rengel 2007). However, the role of litter in directing community dynamics is poorly understood (Bobbink et al. 1988; Heil and Bruggink 1987). In spite of the potential for manipulating litter to amend various ecological processes to direct succession and invasion, it is not a consideration in most management programs.

Many studies have investigated the responses of individual species to application of litter, litter leachate, or both (Putnam and Weston 1986). In most cases, litter, an allelopathic chemical, or both creates a negative response





a.



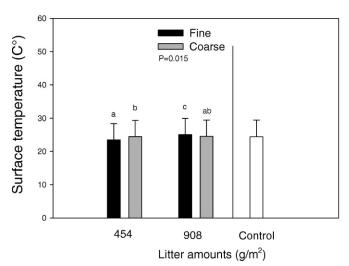


Figure 5. The interaction of year and litter amount in illumination received beneath the litter layer on the day litter was applied (a) and the interaction of year and litter type in illumination received beneath the litter layer on the day litter was applied (b). Means followed by the same letter are not significantly different. Error bars equal the SEM (n=4).

Figure 6. Interaction of litter amount, litter fragment size, and litter type on soil temperature (a) and the interaction of litter amount and litter fragment size on surface temperature (b). Means followed by the same letter are not significantly different. Error bars equal the SEM (n = 4).

from a desired crop species. Based on these studies and a meta-analysis of litter data found in the literature, the prevailing notion is that litter has more negative effects than positive ones on plants (Xiong and Nilsson 1999). It is possible that individual species' responses to litter do not predict the response of plant communities to litter from either that community or litter from other assemblages of species associated with a particular habitat type.

nity at our study sites. We found that native grass density increased with application of low (454 g/m²) amounts of litter where the grasses were subordinate to common St. Johnswort inside the exclosure. Plots that received low amounts of coarse litter inside the exclosure produced a greater amount of grass tillers/m² than the native grass site produced in the control plots. Because light quantity and quality regulates many aspects of plant growth and development, as well as competitive relationships, decreasing light beneath litter may be playing some role in the responses of native grasses (Bazzaz and Carlson 1982; Schimpf and Danz 1999). We also found canopy (surface) and soil temperatures were lower where

Our data indicate that litter can be managed to favor desired functional groups within the plant commu-

low amounts of fine litter were applied, which could influence the rate of photosynthesis and potentially alter water relations (Facelli and Pickett 1991b; Radosevich et al. 1997). However, because there was only a temperature difference of 1 or 2 C, this may not be biologically significant at our study sites. In spite of the potential of the light and temperature to be related to plant responses to litter applications, we assume many other factors and processes may interact to create a facilitative response in native grass density.

We found that adding native plant litter to the weedy site nearly doubled native grass biomass. Plants, their litter, or both can facilitate a negative response on their neighbors (e.g., allelopathy); however, plants and their litter can also facilitate a very strong positive response to their neighbors. For example, Violle et al. (2006) found a positive response of plant growth, especially early growth, to plant litter. Litter can buffer lethal frosts (Heady 1956; Watt 1974), conserve water during drought (Fowler 1986), or add nutrients (Facelli and Pickett 1991a). In most cases, litter has reduced final biomass of plants by acting as a physical barrier, (Facelli and Pickett 1991b), intercepting light (Goldberg and Werner 1983; Hamrick and Lee 1987), or leaching toxins (Suding and Goldberg 1999). In our case, final biomass production of native plants was higher in plots with native plant litter.

Litter, especially grass litter, often limits forb density by suppressing seedling emergence (Facelli and Facelli 1993; Facelli and Picket 1991a; Heady 1956; Hulbert 1969; Watt 1974). This may explain the apparent reduction in native forb density in response to litter of any quality and quantity in this study. However, plots receiving low amounts of finely fragmented litter and high amounts of coarse litter produced about twice the native forb biomass as found in the non–litter-amended control plots. The physical, chemical, and mechanical barriers litter places on forb germination and emergence can easily explain the reduction in forb density (Bosy and Reader 1996), whereas established forbs may have benefited from litter by the same mechanisms as native grasses.

We did not detect any response of common St. Johnswort to litter applications. Bosy and Reader (1995) found common St. Johnswort was reduced by about 34% when covered with Kentucky bluegrass litter compared to a distilled water control, and emergence was reduced by about 95% with addition of grass litter. In our study, seed germination and emergence of seedlings were either not affected or were not important in maintaining population density and biomass. Bazzaz and Carlson (1982) found that weedy early successional species possessed greater photosynthetic flexibility in response to decreasing irradiance than late successional species. In addition, Ehrenfeld (2003) concluded that invasive exotic species tend to produce litter that decays more rapidly than co-occurring

native species. Rapid decomposition tends to result in higher levels of extractible inorganic N. Invasive plants are often favored in high N environments (Herron et al. 2001; McLendon and Rednete 1991). Any long-term effects of litter management on common St. Johnswort would most likely be a response to an indirect competitive effect of increased native plant density and biomass.

The effects of litter on downy brome were much less clear, but there appeared to be litter treatments that could influence this winter annual negatively. Native, coarse litter decreased downy brome below that of other litter treatments. Because perennial grasses tended to be favored by native plant litter, the negative effects of coarse native litter may be related to seed germination and emergence (Reader 1991), which may not influence tiller production in perennial grasses.

Because species availability, species performance, and site availability are three primary causes of succession (Krueger-Mangold et al. 2006), addressing these three causes through litter management may have the potential to shift the successional trajectory toward a desired plant community. In our study, common St. Johnswort was not affected by any litter combination treatment compared to other functional groups. However, adding native litter to the weedy site nearly doubled native grass biomass compared to control, whereas adding high amounts of either litter type or size reduced native grass density by 70% on the native site. Furthermore, native forb density was also reduced by 35% on plots receiving any amount or size combination of litter compared to the control on the native site. Manipulating the type, amount, and texture of litter may be effective tools for increasing native grasses within weedinfested plant communities. Although the addition of litter did not reduce the density or biomass of common St. Johnswort in our study, manipulating litter to increase native grasses and forbs (i.e., species performance) in conjunction with other tools (e.g., herbicides, biocontrol, etc.) may offer potential to shift invasive plant communities toward those that are desired.

Sources of Materials

¹ Phytotronics illuminance meter, Model FCM-10-M, Hummert International, Earth City, MO.

² SAS 9.2 software, SAS Institute, Cary, NC.

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